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Hormonal Independence of Courtship Behavior in the Male Garter Snake

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Garter snakes exhibit a dissociated reproductive tactic in which gonadal activity is minimal at the time of mating, increasing only after the breeding season has ended. Experiments are presented demonstrating that neither short-term nor long-term castration affects courtship behavior in adult male red-sided garter snakes (*Thamnophis sirtalis parietalis*). So long as males have passed through a low-temperature dormancy period (hibernation), castration either shortly after emergence in the spring, or before entering winter dormancy in the fall, does not prevent the display of intense courtship behavior on emergence. Similarly, males castrated during mating activity the previous spring prior to the annual testicular growth phase actively courted females on emergence from hibernation. Males adrenalectomized and castrated during low-temperature dormancy also courted females on emergence. Hypophysectomy during or before low-temperature dormancy did not prevent males from displaying high-intensity courtship behavior on emergence from hibernation. Treatment with sex steroid hormones, as well as hypothalamic and pituitary hormones, and a variety of neural and metabolic affectors also fails to elicit courtship behavior in noncourting males during the summer. It was concluded that causal mechanisms controlling courtship behavior in the red-sided garter snake are fundamentally different, at least at the physiological level, from those mechanisms described for many laboratory and domesticated species.

In the majority of seasonally breeding vertebrates that have been studied to date, gametes are produced during or immediately before breeding (van Tienhoven, 1983). During this period, circulating sex steroid hormones are at their highest levels. A large volume of experimental evidence indicates that in species exhibiting this pattern of gonadal activity in relation to breeding, which may be referred to as an associated reproductive tactic (Crews, 1984), expression of mating behavior depends on gonadal hormones.

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In marked contrast, many species of snakes (Saint-Girons, 1982; Crews, 1983), turtles (Lofts, 1977; Licht, 1984; Crews, 1984), and bats (Gustafson and Shemesh, 1976) produce gametes only after breeding activity has ended; at the time of mating, the gonads are small and the circulating concentrations of sex-steroid hormones are low. This pattern of gonadal activity in relation to breeding may be referred to as a dissociated reproductive tactic (Crews, 1984). Little is known about the mechanisms underlying mating behavior in such species (Camazine, Garstka, Tokarz, and Crews, 1980; Garstka, Camazine, and Crews, 1982). The present study describes a series of experiments designed to determine the role of testicular, adrenal, and pituitary hormones in the control of mating behavior in the male red-sided garter snake, *Thamnophis sirtalis parietalis*.

GENERAL MATERIALS AND METHODS

Animals, housing, and maintenance. Adult garter snakes were captured during field trips in May 1980 and 1983 or purchased from William A. Lemberger Associates, Ltd. (Germantown, Wisc.) in September 1981 and 1982. All snakes, including those obtained commercially, were caught in the Interlake region of Manitoba, Canada.

Housing, maintenance, and environmental conditions were as described previously (Camazine *et al.,* 1980). All experimental manipulations, including anesthesia, surgery, and physiological measurements were as described by Camazine *et al.* (1980).

Hormone treatment. In all castration–androgen replacement experiments, hormone administration was via subcutaneous implantation of Silastic (Dow Corning) capsules (0.058 in. i.d. × 0.077 in. o.d. × 2 cm long) containing crystalline testosterone.

Stimulus females used in behavioral tests were treated daily with a subcutaneous injection of estradiol benzoate (40 μg/75 g body wt) in Steroid Suspending Vehicle for 7 days (Kubie, Cohen, and Halpern, 1978a; Ross and Crews, 1977). Females were used as stimulus animals for only 7 days beginning on the fifth day of injection (Camazine *et al.,* 1980).

Behavioral testing. The courtship and copulatory behavior of garter snakes is easily identified (Noble, 1937; Blanchard and Blanchard, 1941; Crews, 1976; Ross and Crews, 1978). Briefly, male courtship behavior is mediated by the tongue-flick delivery of chemical cues to the vomeronasal organs (Kubie, Vagvolgyi, and Halpern, 1978b). If the female is sexually attractive, the frequency of tongue flicking will increase and the male will align his body with the female's body. The male will then begin to press his chin against the female's back and repeatedly and rapidly traverse her length. The male will then begin to exhibit caudocephalic and cephalocaudal contractile waves along the length of his body. This behavior may continue for many minutes before the male attempts cloacal apposition by maneuvering his tail beneath the female's tail. If the female is sexually receptive she will lift her tail and gape her cloaca, enabling the male to insert one of two hemipenes.

Because courtship behavior in the male is a cumulative continuum of specific behaviors, it is possible to assign males a score based on a graduated scale from 0 to 3 (in increments of 0.5) with 0 being failure of the male to approach the female and 3 being an attempted intromission (Table 1). Courtship is the only context in which chin-rubbing behavior is exhibited. Therefore, in these studies chin-rubbing behavior was used as a criterion of courtship; intense courtship was defined operationally as a score of 1.5 or greater.

Males were housed in isolation and tested in their home cage. Behavioral tests consisted of presenting two stimulus females in succession for 2 min each. Tests were conducted daily between 1200 and 1400 hr. The order of presentation of stimulus females was alternated daily. The identity of the males was not determined until the end of testing.

Statistics. Analysis of parametric data was based on common measures of central tendency and dispersal. Analysis of variance (ANOVA) was used to determine significant treatment effects. If ANOVA was significant ($P < 0.05$), the Student–Newman–Keuls' test (SNK) was used to test for between-group differences. Student's t test was used to test for significant differences between two means. Nonparametric, ordinal-scored data (e.g., Fig. 1) are displayed as group medians. Using a chi-square test of goodness of fit, the distribution of these median scores did not significantly deviate from normality ($\chi^2 = 1.22$, $P > 0.5$). Analysis of these groups of ordinal-scored data was by comparison of a parametric

TABLE 1

Graduated Scale of Courtship Behavior in the Male Red-Sided Garter Snake, *Thamnophis sirtalis parietalis*

Courtship score	Behavioral description
0.0	Male either fails to investigate female or investigates only initially.
0.5	Male tongue-flicks and chin-rubs female after initial investigation.
1.0	Male's chin is in contact with female for entire courtship test or male courts female at a higher level but becomes distracted from courting.
1.5	Male is aligned along and covers female's back while moving slowly with female; male is not distracted from courting.
2.0	Male behaves as 1.5 above but also exhibits rapid and repeated traverses along the length of female's body and/or contractile waves along the length of his body.
2.5	Male behaves as 2.0 but also attempts cloacal apposition by maneuvering his body and/or tail under female's body and/or tail.
3.0	Male vigorously attempts intromission by rolling female; mating.

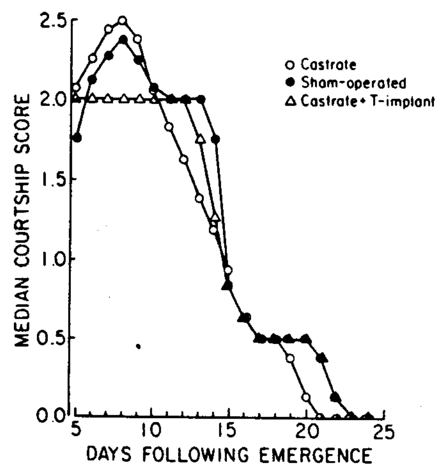

FIG. 1. Changes in courtship behavior of male red-sided garter snakes (*Thamnophis sirtalis parietalis*) on emergence from low-temperature dormancy. In nature following hibernation, or in the laboratory following low-temperature dormancy, courtship behavior initially is vigorous but then gradually declines in intensity; males will not exhibit courtship behavior again unless exposed to cold temperatures. Depicted here is the decline in courtship behavior in males that were castrated, castrated and given testosterone replacement therapy, or sham-operated in the fall prior to entering winter dormancy.

component: individual latency to decrease to a score not higher than a stated level. The value of the test statistic and the probability value are given for each calculation; a value of $P < 0.05$ was required for significance.

EXPERIMENT 1

Effect of Castration before Hibernation on Male Courtship Behavior

A previous study (Camazine *et al.*, 1980) indicated that castration at the time of emergence from low-temperature dormancy has no effect on expression of male courtship behavior. Males castrated on the fifth day after emergence from dormancy court females as actively as do intact males. Furthermore, males given androgen replacement therapy at the time of castration showed the same decline in courtship behavior as untreated castrates and sham-operated males.

These results indicate that androgen is not required at the time of mating, but it is possible that the brain mechanisms that underlie male courtship behavior in the red-sided garter snake are activated by androgens during winter dormancy. Activation of the neural substrates of male courtship behavior during dormancy is suggested by the finding that males court more actively the longer they are in low-temperature dormancy (Garstka *et al.*, 1982). To test this hypothesis, male *Thamnophis sirtalis parietalis* were either castrated, castrated and given testosterone replacement, or sham-operated (n = 10 per group) 3 weeks prior to entering low-temperature dormancy. After 8 weeks of low-temperature dormancy, the males were removed from the coldroom, placed in summer-like conditions, and tested for courtship behavior daily for 24 days.

Results. All males courted the stimulus females following emergence from low-temperature dormancy. There was no difference among the groups in the intensity of courtship behavior exhibited ($F = 0.74$, $P > 0.25$) nor in the pattern of decline in courtship behavior over time (Fig. 1).

EXPERIMENT 2

Effect of Castration before the Preceding Testicular Growth Cycle on Male Courtship Behavior

It is possible that courtship behavior in males is primed by the elevated concentration of androgens that occur during the testicular growth cycle of the preceding year. To test this hypothesis, males were treated during the breeding season of the preceding year before the period of testicular growth that follows the end of sexual activity. Most males ($n = 14$) were collected from mating balls in the field during the first 3 days of the emergence period. Other males ($n = 6$) were obtained from P. Licht (University of California, Berkeley) following their emergence from artificial hibernation. In both instances surgery confirmed that testicular recrudescence had not yet begun in the males. Males were either castrated, castrated and given testosterone replacement therapy, or sham-operated.

Males were maintained in the laboratory for 5 months under summer-like conditions before being subjected to low-temperature dormancy. After 10 weeks of dormancy, the males were removed from dormancy and the surviving animals tested for courtship behavior daily for 10 days.

Results. All males exhibited chin-rubbing on at least 8 of the 10 days of behavioral testing that followed emergence (Table 2).

TABLE 2

Effect of Castration before the Preceding Testicular Growth Cycle on Courtship Behavior in Male Red-Sided Garter Snakes (*Thamnophis sirtalis parietalis*)[a]

Group	Number of tests	Behavioral test score		
		0.0	≥0.5	≥1.5
Castrate ($n = 7$)	137	23	77	26
Castrate + testosterone ($n = 7$)	140	21	79	54
Sham control ($n = 6$)	120	32	68	28

[a] Percentage of behavioral tests on which different courtship scores were achieved are shown.

EXPERIMENT 3

Effect of Exogenous Androgen Administration on Noncourting Males during the Summer

In an earlier paper (Crews, 1976) it was reported that implantation of testosterone stimulated courtship behavior in *T. s. sirtalis*. However, it is important to examine the experimental paradigm used. In that study animals ($n = 6$) were obtained in November and immediately placed in a low-temperature coldroom for 4 months. Animals were then transferred to summer-like conditions where they were tested daily for 2 weeks. Within 4 days of emergence from low-temperature dormancy all males were observed to court. The onset of courtship behavior coincided with the implantation of androgen and further, the subsequent decline in courtship behavior corresponded with the removal of the implant. This correlation of events was taken as evidence for a deterministic relationship between androgens and courtship behavior. This interpretation must be questioned since adequate controls were not run due to the availability of the animals at the time. Thus, in that study all males were given an implant of androgen on emergence; none of the males were left untreated and only one male was successfully castrated. In light of the results obtained from the castration–androgen replacement experiments, and considering that in nature and in the laboratory courtship behavior (i) is initiated 2–4 days after emergence, (ii) lasts for only a short period before declining, and (iii) does not recur unless the male undergoes another period of low-temperature dormancy, we sought to determine the effects of exogenous androgens on the behavior of males that have gone through the courtship phase and no longer responded to stimulus females.

Courting males were captured in the field in May 1983, and transported to the laboratory where they were housed under summer-like conditions. In mid-July each male was tested with 10 stimulus females. None of the males were observed to court any of the stimulus females, a finding consistent with previous work in this and other laboratories. Males were then divided into four experimental groups: (i) intact males receiving an empty implant ($n = 11$); (ii) intact males receiving a testosterone implant ($n = 13$); (iii) castrated males receiving an empty implant ($n = 11$); and (iv) castrated males receiving a testosterone implant ($n = 13$). Behavioral testing commenced the day following surgery and lasted for 6 weeks.

Results. None of the males in any of the four experimental groups received a score above 0.0 at any time during the 6 weeks of testing.

EXPERIMENT 4

Effect of Castration and Adrenalectomy on Male Courtship Behavior

The adrenal gland also produces sex steroid hormones that have been implicated in the control of courtship behavior (Brain, 1979). Although castrated males in Experiments 1 and 2 still had measurable serum androgens (Table 3), there was no evidence of compensatory adrenal hypertrophy. Relative adrenal weights were not significantly different among the groups of males castrated on emergence ($F = 0.81$, $P > 0.25$) (Camazine *et al.*, 1980), or among the groups of males castrated during the breeding season of the previous year before testicular growth had begun ($F = 0.24$, $P > 0.5$). However, to examine the possibility that adrenal hormones may activate courtship behavior in males, an experiment was conducted in which males were castrated or castrated and adrenalectomized immediately on emergence from 10 weeks of low-temperature dormancy. Unlike in the other experiments in which males were given graded courtship scores, in this experiment males were evaluated according to whether or not they achieved a score of 1.5 or greater in each behavioral test.

Results. Four of the six male garter snakes that had both their adrenals and their testes removed exhibited intense courtship behavior (defined as a score of 1.5 or greater) on emergence; one of the two males that failed to court died 7 days following the operation. All three of the castrated males exhibited intense courtship behavior on emergence.

EXPERIMENT 5

Effect of Hypophysectomy on Male Courtship Behavior

Since we could find no evidence indicating that the testes or the adrenals are necessary for courtship behavior in the adult male red-sided garter snake, we hypothesized that pituitary secretions might be involved in

TABLE 3
Serum Androgens of Male Red-Sided Garter Snakes (*Thamnophis sirtalis parietalis*) in Different Experiments

Experiment	Group	*n*	Serum androgens (ng/ml)
Castration following hibernation[a] (Day 37)	Castrate	5	0.85 ± 0.14
	Sham-operated	5	3.75 ± 0.55
Castration before entering hibernation (Day 27)	Castrate	10	0.13 ± 0.27
	Sham-operated	10	1.44 ± 0.31
Castration during previous breeding season (Day 24)	Castrate	7	0.25 ± 0.21
	Sham-operated	6	1.16 ± 0.30
Hypophysectomy during hibernation (Day 24)	Hypox	4	0.10 ± 0.21
	Sham-operated	5	0.30 ± 0.39
Hypophysectomy before entering hibernation (Day 24)	Hypox	4	0.58 ± 0.51
	Sham-operated	4	1.32 ± 0.19

Note. Snakes in all groups exhibited courtship behavior upon emergence from dormancy that did not significantly differ. Time of bleeding (days post-emergence) shown in parentheses.
[a] Data from Camazine *et al.*, 1980.

TABLE 4
Effect of Hypophysectomy on Courtship Behavior of Male Red-Sided Garter Snakes (*Thamnophis sirtalis parietalis*)[a]

Time of hypophysectomy	Number of tests	Behavioral test score 0.0	≥0.5	≥1.5
During low temperature dormancy				
Sham-operated males (n = 5)	170	31	69	26
Hypophysectomized males (n = 5)	170	22	78	40
Before entering low-temperature dormancy				
Sham-operated males (n = 4)	44	59	41	0
Hypophysectomized males (n = 4)	44	45	55	10

[a] Percentage of behavioral tests on which different courtship scores were achieved are shown.

the control of courtship behavior. In one experiment males were hypophysectomized or sham-operated during low-temperature dormancy immediately before their emergence (n = 5 per group). In a second experiment, males were either hypophysectomized or sham operated prior to dormancy (n = 6 per group). After 8 weeks of dormancy the surviving animals (n = 4, each group) were tested for sexual activity for 3 weeks.

Results. All animals exhibited intense courtship behavior (scored 1.5 or higher) toward the stimulus females when they emerged from low-temperature dormancy. In the first experiment in which males were operated on during low-temperature dormancy, the groups did not differ in the intensity of courtship behavior (t = 0.24, $P > 0.5$) (Table 4). The groups also did not differ in the time elapsed until courtship declined (Table 5). Similar results were obtained from males operated on before entering low-temperature dormancy although in this experiment the males were not as active as in the previous experiment. The sham-operated

TABLE 5
Decline in Courtship Behavior in Adult Male Red-Sided Garter Snakes (*Thamnophis sirtalis parietalis*) following Emergence from Hibernation

Treatment	n	Days for courtship to decline to a score of: 1.5	1.0
Sham-operated males	5	12.8 (2.6)	14.8 (1.6)
Hypophysectomized males	5	14.8 (2.8)	16.0 (3.2)
Significance		t = 0.53, $P > 0.5$	t = 0.33, $P > 0.5$

Notes. Males were hypophysectomized or sham operated during low-temperature dormancy. Mean and standard error shown.

TABLE 6
Effect of Hypophysectomy during or before Low-Temperature Dormancy on the Testes and Adrenals in the Red-Sided Garter Snake, *Thamnophis sirtalis parietalis*

Time of hypophysectomy		Gonadosomatic index	Adrenosomatic index
During low-temperature dormancy			
Sham-operated males	5	0.54 (0.07)	0.32 (0.02)
Hypophysectomized males	5	0.19 (0.03)	0.22 (0.02)
Before entering low-temperature dormancy			
Sham-operated males	4	0.62 (0.08)	0.70 (0.05)
Hypophysectomized males	4	0.48 (0.10)	0.50 (0.05)

Notes. Shown are mean gonadosomatic index (right testis weight/total body weight × 100) and adrenosomatic index (paired adrenal weights/total body weight × 1000). Standard error shown in parentheses.

and hypophysectomized males were not different in the intensity of courtship behavior exhibited on emergence ($t = 0.26$, $P > 0.5$) (Table 4). In both experiments relative adrenal weights, an index of the completeness of hypophysectomy, were significantly different between the hypophysectomized and sham-operated groups ($t = 3.25$, $P < 0.02$; $t = 4.25$, $P < 0.01$, respectively) (Table 6).

DISCUSSION

Traditionally, two lines of evidence are considered sufficient proof that gonadal hormones are involved in the control of mating behavior. First, removal of the gonads must result in a decline or cessation of mating behavior. Second, replacement of the hormones produced by the gonads must restore or maintain mating behavior in gonadectomized individuals. The present study shows clearly that in the red-sided garter snake, neither of these conditions are met. Castration, even for a prolonged period, will not prevent males from exhibiting mating behavior if they have undergone low-temperature dormancy. Further, treatment with exogenous androgen fails to elicit mating behavior when administered to castrated or intact individuals maintained on summer-like conditions.

While these results suggest that in the adult male red-sided garter snake the exhibition of courtship behavior is independent of testicular, adrenal, and pituitary hormones, this does not necessarily mean these hormones never influence courtship behavior. It is possible that exposure to gonadal hormones at a specific period of development may organize the neural substrates of courtship behavior such that in the adult, the change in environmental temperature, and not a change in hormone concentration in the circulation, activates mating behavior. In northern temperate climates, garter snakes have at most 4 months in which to mate, reproduce, and replace depleted fat stores before re-entering the underground hibernacula. Such a hormone-induced, temperature-sensitive mechanism would enable mating to occur immediately on emergence instead of 6 weeks later, the time required for the gametes to mature.

The breeding season in garter snakes in Canada and the northern United States occurs in the spring shortly after emergence from winter (low-temperature) dormancy (Gregory, 1976). Male courtship behavior is stimulated by exposure to warm temperatures (Hawley and Aleksiuk, 1975, 1976). The breeding season is brief, lasting for as little as 4 days. Annual testicular growth occurs 6 weeks later, after all sexual activity has ceased (Gregory, 1976; Crews, 1983; Crews and Garstka, 1982). Spermatozoa are evacuated from seminiferous tubules into the ductuli deferentia in late summer, and are stored there until the following spring. Thus, throughout the period of winter dormancy and mating, the testes contain only spermatogonia and spermatocytes and are significantly smaller than during the recrudescence phase that follows breeding (Fox, 1952, 1954; Gregory, 1976; Licht, 1983). Circulating androgen levels during the breeding season are less than one-tenth of those observed during testicular recrudescence (Camazine *et al.*, 1980; Garstka and Crews, 1982; D. Crews, unpublished data).

A similar pattern of initially vigorous courtship behavior that declines over subsequent weeks can be evoked in the laboratory. Males that have been exposed to at least 7 weeks of low-temperature dormancy (5°C) exhibit intense courtship behavior for approximately 2 to 3 weeks when transferred to warm, summer-like conditions (Garstka *et al.*, 1982). Experiments indicate the decline in courtship behavior is not due to habituation to females. Intact males exposed daily to females exhibit a level of courtship behavior that is equal to that of males kept isolated after emergence and then tested with two stimulus females (Aleksiuk and Gregory, 1974; Camazine *et al.*, 1980). As in nature, laboratory-hibernated males also exhibit testicular growth subsequent to the cessation of courtship behavior; further, the stored sperm disintegrate and new testicular growth begins at the appropriate time post-emergence regardless of whether males mate (Camazine *et al.*, 1980), indicating these events to be independent of mating. Following the initial period of intense sexual activity, males will not exhibit courtship behavior again unless exposed to a prolonged period of low temperatures (D. Crews, unpublished data).

Other studies have supported the finding that it is impossible to prevent male garter snakes from exhibiting courtship behavior on emergence from low-temperature dormancy. For example, males treated with cyproterone acetate while in low-temperature dormancy (6/6) show normal levels of courtship behavior on emergence 1 week later (D. Crews, unpublished data). Nor have we found evidence that other sex steroid hormones will activate courtship behavior in males maintained under summer-like conditions. For example, male *T. radix*, a close relative to *T. s. parietalis*, fails to respond to implants containing either estradiol-17β, dihydrotestosterone, or dihydrotestosterone and estradiol in combination (B. Camazine and D. Crews, unpublished data). In this latter study the implants remained *in situ* for 25 days with daily behavioral tests commencing 5 days after implantation. None of the hormone treatments restored courtship behavior ($F = 0.12$; $P > 0.5$). These negative results are similar to those obtained in other studies (Garstka *et al.*, 1982) in which behaviorally inactive male garter snakes were given arginine-8-vasotocin, a pituitary hormone important in the regulation of courtship behavior in the rough-skinned newt (Moore and Zoeller, 1979). Systemic administration of a variety of brain hormones such as luteinizing hormone-releasing hormone and melatonin, and catecholamine neurotransmitters, including dopamine, epinephrine, norepinephrine, and serotonin, have also failed to stimulate male courtship behavior in behaviorally inactive males (Garstka *et al.*, 1982). Finally, injection of substances whose levels differ markedly between the dormant and active periods (Aleksiuk and Stewart, 1971; Aleksiuk, 1976), such as thyroxine, glucose, and electrolytes, have also failed to elicit any behavioral response in behaviorally inactive male garter snakes (Garstka *et al.*, 1982).

It is significant that the red-sided garter snake exhibits a dissociated reproductive tactic in which gonadal activity (gametogenesis and maximum sex steroid secretion) occurs only after all mating behavior has ceased; the gametes produced are then stored in accessory sex structures until the following breeding season. The studies reported here show clearly that the causal mechanisms controlling courtship behavior in the male garter snake are fundamentally different, at least at the physiological level, from those with which we are familiar in laboratory and domesticated vertebrates. It is likely that other species that exhibit a dissociated reproductive tactic also differ in fundamental ways from more commonly studied vertebrates. For example, hormonal independence of courtship and copulatory behavior is likely to exist in some species of hibernating bats. In the little brown bat (*Myotis lucifugus*) spermatogenesis and maximum androgen secretion occurs in the summer, whereas mating occurs in the winter (Gustafson and Shemesh, 1976; Damassa, Gustafson, and King, 1982). The female Asian musk shrew (*Suncus murinus*) also shows a dissociated reproductive tactic. In this species ovarian growth depends on mating stimulation (Dryden, 1969; Dryden and Anderson, 1977). Experiments have demonstrated that in the musk shrew development of accessory sex characters, including behavior, are independent of ovarian hormones (Dryden and Anderson, 1977). A similar phenomenon has been observed in female garter snakes (Licht and Bona-Gallo, 1982; W. Garstka and D. Crews, unpublished data). Finally, species need not exhibit a dissociated reproductive tactic to show androgen independence of male courtship behavior as demonstrated by Moore and Kranz (1983) with the white-crowned sparrow.

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